TAXONOMY OF *CYPHOMERIS* (NYCTAGINACEAE) BASED ON MULTIVARIATE ANALYSES OF GEOGRAPHIC VARIATION

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ABSTRACT

The two species of *Cyphomeris* (Nyctaginaceae) occur in arid regions of central southern North America. Historically, *C. gypsophiloides* (Mart. & Gal.) Standl., the more widespread, consisted of two subspecies. The other, *C. crassifolia* (Standl.) Standl., is restricted to the eastern margin of the range of the genus. A survey of herbarium specimens reveals considerable variation particularly in fruit characteristics, leaf shape, and foliar pubescence and some intergradation in these features among populations. We used 114 specimens and 29 population samples to examine relationships of 14 vegetative and 10 fruit characters. Cluster analysis, principal components analysis, discriminant analysis, and multivariate analysis of variance indicate the presence of two morphological groups that correspond roughly to the species-level taxa of previous authors, groups that can be separated by morphology, geography, and ecology. These two species are maintained. The sole infraspecific taxon, *C. gypsophiloides* var. *stewartii* I. M. Johnst., is noted to be an extreme and geographically restricted form intergradient with nearby populations and is not recognized taxonomically.

RESUMEN

La variación geográfica de macromorfologia de *Cyphomeris*, un género pequeño de Nyctaginaceae de zonas áridas de la parte sur-centro de Norte América, fue examinada mediante el uso de métodos estadísticos multivariantes. Autores anteriores reconocieron dos especias, una [*C. gypsophiloides* (Mart. & Gal.) Standl.] con dos subespecias, y la otra [*C. crassifolia* Standl.] restringida a la parte este del área del género. Usamos 114 muestras y ejemplares de 29 poblaciones para revisar las afinidades de 14 caracteres vegetativos y 10 caracteres de los frutos. Los datos fueron analizados por análisis de agrupación, análisis de componentes principales, análisis discriminante, y análisis de multivariante. Los resultados indican la presencia de dos grupos morfológicos que se corresponden aproximadamente con los taxa delnivel de especie de los autores anteriores; que pueden ser separadas por su morfología, geografía, y ecología. Unicamente no se reconoce el taxon infraespecifico, *C. gypsophiloides* var *stewartii* I. M. Johnston, pero es considerado como una forma extrema, intermedia con poblaciones más o menos aisladas en las montañas próximas.

INTRODUCTION

Cyphomeris Standl. (Nyctaginaceae) is a small genus of perennial herbs distributed in arid and semi-arid regions of northern Mexico and the southwestern United States. It has been considered a subgenus of *Boerhavia* L.

SIDA 16(4): 679–697. 1995

(Fosberg 1978). Standley (1911) and Reed (1970) recognized two species, *C. gypsophiloides* (Mart. & Gal.) Standl. and *C. crassifolia* (Standl.) Standl., distinguished by leaf shape, leaf pubescence, and features of the fruit, each having a geographic range more or less exclusive of the other. I. M. Johnston (1944) described a third taxon, *C. gypsophiloides* var. *stewartii*, from La Sierra el Diablo in southeastern Chihuahua, noting its robust habit and glandular hairs. He refrained from describing it at specific rank because he thought collections of *C. gypsophiloides* var. *gypsophiloides* from extreme southwestern Coahuila were transitional to it.

The two species of *Cyphomeris* are not completely distinguishable morphologically. There is a wide range of variation (Fig. 1) within and between species, some apparently more or less continuous, other clearly discontinuous. The geographic limitation of the genus to an ecologically definable region and fragmentation of populations according to available habitat allows an assessment of relationships of morphological variation to geography and topography throughout the range of the genus. These results were used to examine the significance of the characters used by previous authors in the delimitation of species of *Cyphomeris*, and to aid in our own taxonomy of the genus.

CHARACTERISTICS OF POPULATIONS AND POLLINATION

Throughout much of its range, and particularly west of the Sierra Madre Oriental, *Cyphomeris* often exists in small groups of 20–30 individuals confined to rocky soils of road cuts, washes, and other rough terrain, generally separated from other such groups by large distances. Thus, the overall population is highly subdivided and the majority of outcrossing probably occurs between genetically related individuals. In addition, moderate to high levels of self fertilization also occur. Monitoring of a natural population of *Cyphomeris* in southern New Mexico indicates that plants produce fruits from all or mostly cleistogamous flowers during the dry months (typically May–July) of the growing season (Fig. 2). After the onset of summer rains (typically July–September) plants produce mostly or all chasmogamous flowers. In each of two growing seasons mean percentage of cleistogamous flowers began at 100%, their relative frequency decreasing as the season progressed, corresponding to an increase in precipitation. Pooled data (across years) reveals a significant correlation (r = -0.74, $P < 0.05$) between the mean percentage of cleistogamous flowers and cumulative rainfall.

Chasmogamous flowers, about a centimeter across and varying from deep to pale pink or rarely nearly white, are visited by small bees, flies, and butterflies during early morning hours. Insects tend to move from flower to flower on the same plant, afterward moving to a nearby plant where the pattern of intraplant visitation often is repeated. Whether or not a flower is

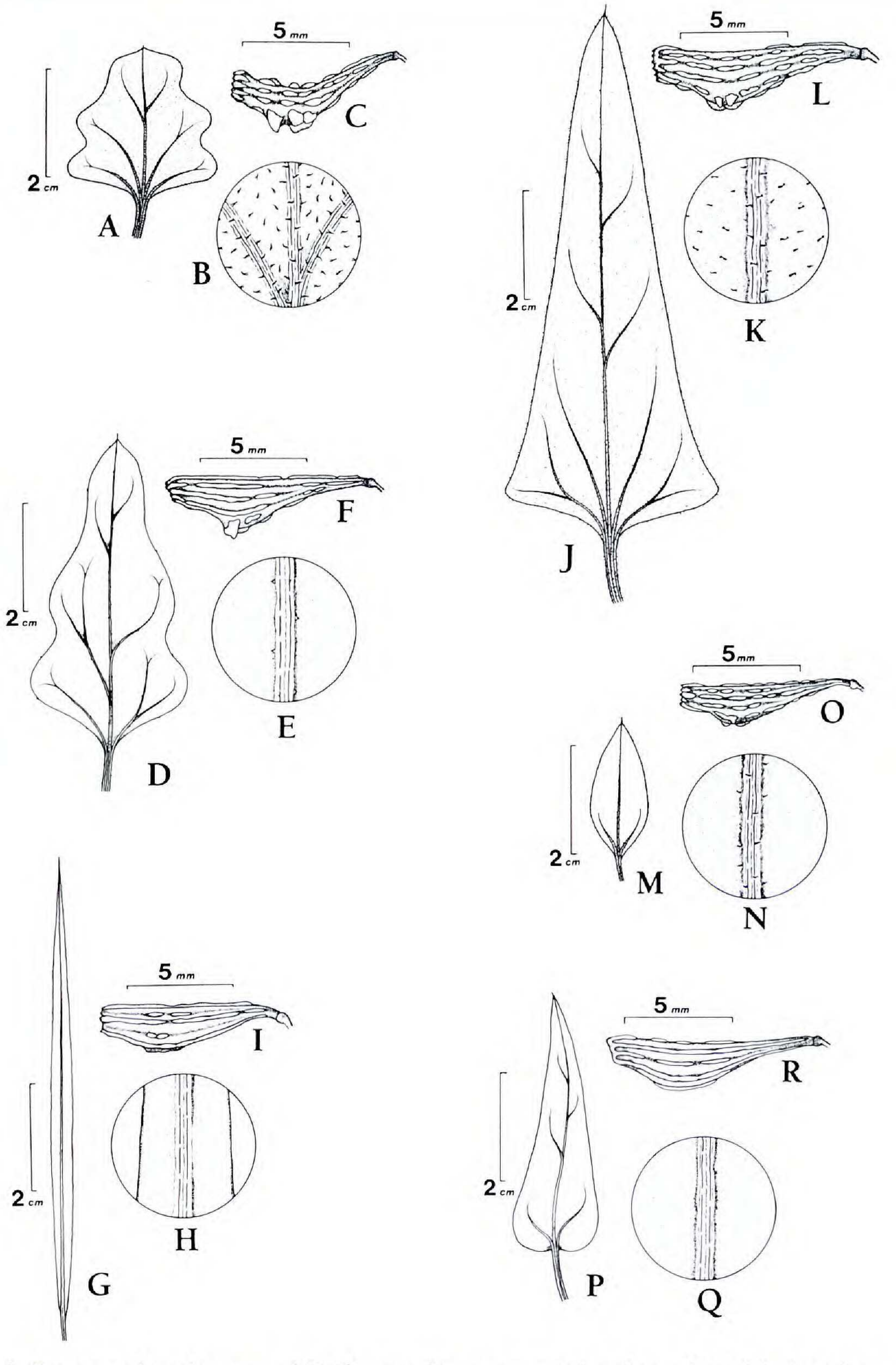

FIG. 1. Leaves and anthocarps of *Cyphomeris*. Figures in circles show abaxial leaf surface at 40. Sample numbers are given in parenthesis and associate drawings with vouchers listed in Appendix A and localities on map (Fig. 4); (a-c) *C. crassifolia* (17), (d-f) intergrade from western Texas (8), (g-i) linear-leaved example of *C. gypsophiloides* (24), (j-l) *C. gypsophiloides* var. *stewartii* (25), (m-n) intergrade from central San Luis Potosi (20), (p-r) *C. gypsophiloides* (29).

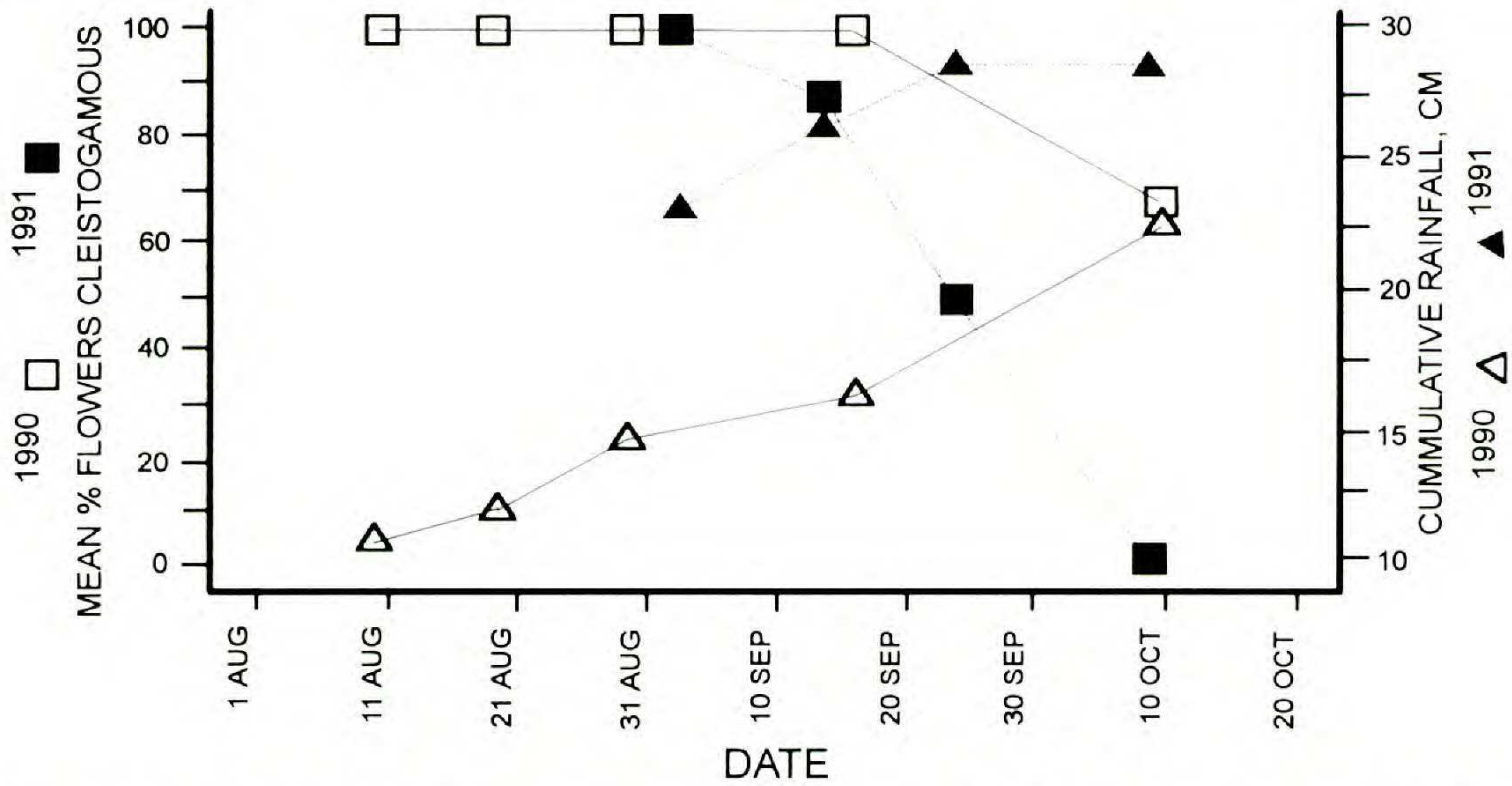

FIG. 2. Plots showing the relationship between the mean percentage of flowers that are cleistogamous (squares) and cumulative rainfall (triangles) in a population of *Cyphomeris gypsophiloides* located along the W slope of the Organ Mountains, approximately 16 km E of Las Cruces, New Mexico.

visited , the stamens of chasmogamous flowers curl over the style and stigma by late morning. This process has been described for similar flowers in the nyctage genera *Acleisanthes* and *Ammocodon* (Spellenberg and Delson 1977), *Boerhavia* (Chaturvedi 1989), and *Mirabilis* (Cruden 1973; Hernandez 1990). It results in self-pollination and seed set in all species examined in these genera that have cleistogamous flowers. We have no reason to suspect otherwise for *Cyphomeris*.

Such observations suggest that selfing often constitutes a major mode of reproduction in *Cyphomeris*, particularly in dry years or areas of low annual rainfall. As a result, the level of inbreeding is likely higher than that implied by population substructure, a situation conducive to rapid and local differentiation by the combined action of genetic drift and selection (Wright 1938, 1940, 1943).

MATERIALS AND METHODS FOR MULTIVARIATE ANALYSES

Data for numerical analyses were obtained from two sources. The first consists of 297 collections from 15 herbaria, including all holotypes. Of these specimens, 114 represented the genus well geographically, possessed complete location data, and exhibited all characters selected for analyses. Only these specimens (OTU's) were measured (Mahrt 1993).

In addition to the herbarium specimens, 29 population samples were collected from most of the range of the genus (Appendix A). Each collection represents a distinct locality and consists of 6–10 branches, each broken at the base of a different plant. Vouchers are at NMC, with duplicates variously distributed to ARIZ, ASU, BRIT, CIIDIR, ENCB, F, IBUG, IEB, MEXU, MO, MT, NMC, NY, SLPM, TEX, UC, US (Holmgren et al. 1990).

Data were taken on 14 vegetative and 10 fruit characters (Appendix B). Characters included those considered diagnostic by previous authors as well as those known to exhibit geographic variation. Although statistical problems are known to occur with their use (Phillips 1983), two ratios (MLR and ULR) were included since they provided the best measure of important aspects of leaf shape. Each character was measured an average of three times at different locations on each specimen and a set of character means was computed for each specimen. These were used for all numerical analyses. Character measurements were confined to mature organs that did not represent infrequent extremes for a specimen. Characters were measured with an ocular rule of 100 units in a dissecting microscope at 10–40. Hair densities (HD and GHD) were the number of hairs occurring in 1.5 x 2 mm rectangle. Data were not transformed since a preliminary analysis of residuals revealed reasonably normal distributions for all characters (including ratios and meristic characters).

OTUs were first assigned to one of three *a priori* categories based on Reed's (1970) taxonomy: 1) *C. gypsophiloides*; 2) *C. crassifolia*; and 3) intergrade. Three OTUs of *C. gypsophiloides* var. *stewartii*, a taxon outside the range of Reed's treatment, were assigned to category one. We use these categories throughout the following analysis.

Data from the 114 herbarium specimens were analyzed in three steps. First we examined relationships among OTUs by centroid hierarchical cluster analysis (CL) of all 24 characters. Next we employed a principal components analysis (PCA) of the character correlation matrix. Finally, we performed an *a posteriori* multivariate analysis of variance (MANOVA) on selected phenetic assemblages (exposed by CL) to identify their distinguishing characters.

Data from the 29 populations were analyzed initially with a procedure outlined by Zimmerman and Ludwig (1975). This procedure employs discriminant analysis (DA) to detect clusters of related sample populations by identifying pairs for which the Mahalanobis distance (D^2) is non-significant. For each pairwise comparison between populations, DA constructs a discriminant function, calculates D^2, and computes an F statistic that tests if D^2 is significantly greater than zero. Population localities then are plotted on a map and pairs for which D^2 is non-significant are connected with lines. Aggregates of associated populations can then be visualized.

Complimentary to DA, a MANOVA was conducted, followed by a multivariate "means separation" technique developed by Smith et al. (1993). In this technique, the population multivariate sample means first are standardized and subjected to a CL. Then a "group" variable is created, each group now treated as a single sample unit. Next, a MANOVA is run to determine if there are significant differences between groups. If differences exist, the CL is consulted and the closest groups (those joined first) are combined into a super group. A nested MANOVA with super groups, and groups within super groups, is then conducted and the significance levels of the resulting tests compared. The test for super groups should indicate significant differences whereas the test for groups within super groups may be either significant or non-significant. If the test is significant, then that is an indication the joining of the most recently combined groups was inappropriate. If the test is not significant, then the super groupings to this point are reasonable and one may proceed to the next joining as indicated by the CL. The end result of this process is the formation of groups of sample populations whose members are homogeneous, but for which there are significant differences between groups.

Analyses were performed using the Statistical Analysis System (SAS) on the mainframe computer of New Mexico State University. Cluster analysis, PCA, DA, and MANOVA were conducted using the CLUSTER, PRINCOMP, DISCRIM, and GLM procedures respectively (SAS Institute 1990). Standardization of sample population means was accomplished using IML (SAS Institute 1989).

RESULTS

The CL of herbarium specimens, using 24 characters, resulted in three major groups of OTUs (Fig. 3, branches A, B, and C). Clusters were arbitrarily defined at approximately 0.90 on the distance scale. One minor cluster (branch D) and four ungrouped specimens are also present at this level. Branch B constitutes a nearly homogenous collection of OTUs of *C. crassifolia*. Branch A contains the majority of *C. gypsophiloides* specimens, but with a mixture of *a priori* classified OTUs from *C. crassifolia* and intergrades. Branch A-1 is mostly OTUs of *C. gypsophiloides* from northern and western areas (Fig. 4, black stars). Branch A-2 is mostly OTUs of intergrades and *C. crassifolia* that are largely southern and eastern in distribution (Fig. 4, open stars). Branch C consists of seven OTUs of linear-leaved forms of *C. gypsophiloides*. Of the three OTUs assigned to *C. gypsophiloides* var. *stewartii*, two from La Sierra el Diablo in southeastern Chihuahua) remain distinct, whereas the third, from the nearby La Sierra el Rosario in northeastern Durango, is grouped with the majority of specimens representing *C. gypsophiloides* (branch A-1).

A dendrogram (Fig. 5) from the CL of standardized population means reveals a pattern similar to that of the CL of herbarium specimens (Fig. 3). Two major clusters and six distinct populations are defined at 0.60 on the

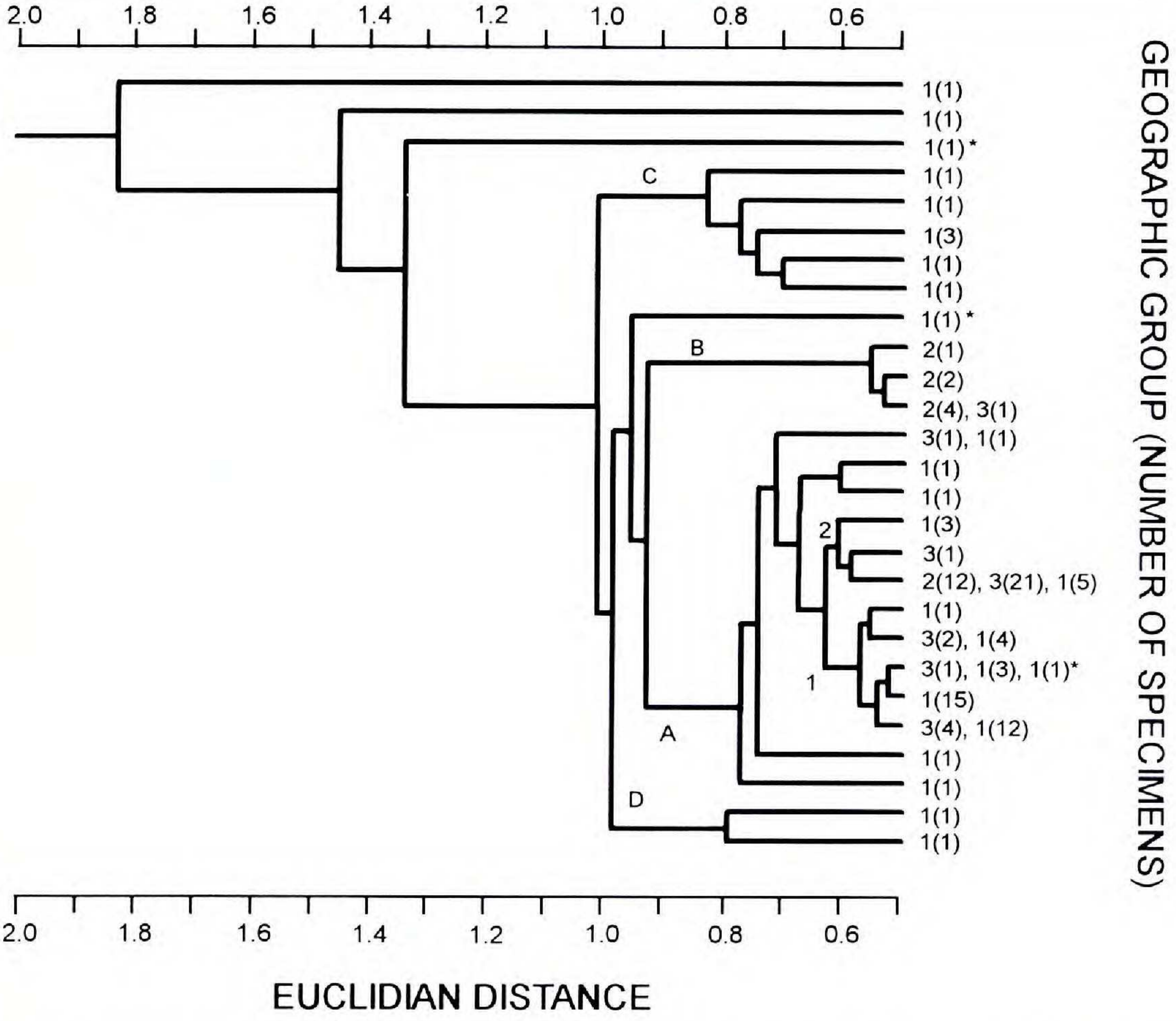

FIG. 3. Partial dendrogram from the cluster analysis of herbarium specimens. Values along the horizontal axis signify the normalized euclidian distance between cluster centroids (SAS Institute 1989). Numbers at the tip of each branch indicate the composition of the specimens contained therein. The first digit refers to *a priori* group (1 = *C. gypsophiloides*, 2 = *C. crassifolia*, 3 = intergrade). The value in parentheses gives the number of specimens belonging to that group on that branch. Clusters discussed in the text are identified by capital letters and arabic numerals near the base of each cluster. An asterisk at the end of a branch signifies an OTU identified as *C. gypsophiloides* var. *stewartii*.

distance scale. Branch A has two subgroups: A-1 has four *C. gypsophiloides* samples, all northern; A-2) has 14 intergrade populations and a single sample representing *C. gypsophiloides* var. *stewartii*. Four samples of *C. crassifolia* comprise branch B. Three unclustered populations of linear-leaved *C. gypsophiloides* form branch C at 0.90 on the distance scale, implying a loose but explicit morphological relationship. The remaining samples, one each of *C. gypsophiloides*, *C. crassifolia*, and *C. gypsophiloides var. stewartii,* join after the major branches A, B, and C have combined. Thus, they have little morphological affinity among themselves or with any of the other populations.

Results from PCA are summarized in Table 1. The first three principal components account for 58.6% of the total sample variance (Component 1

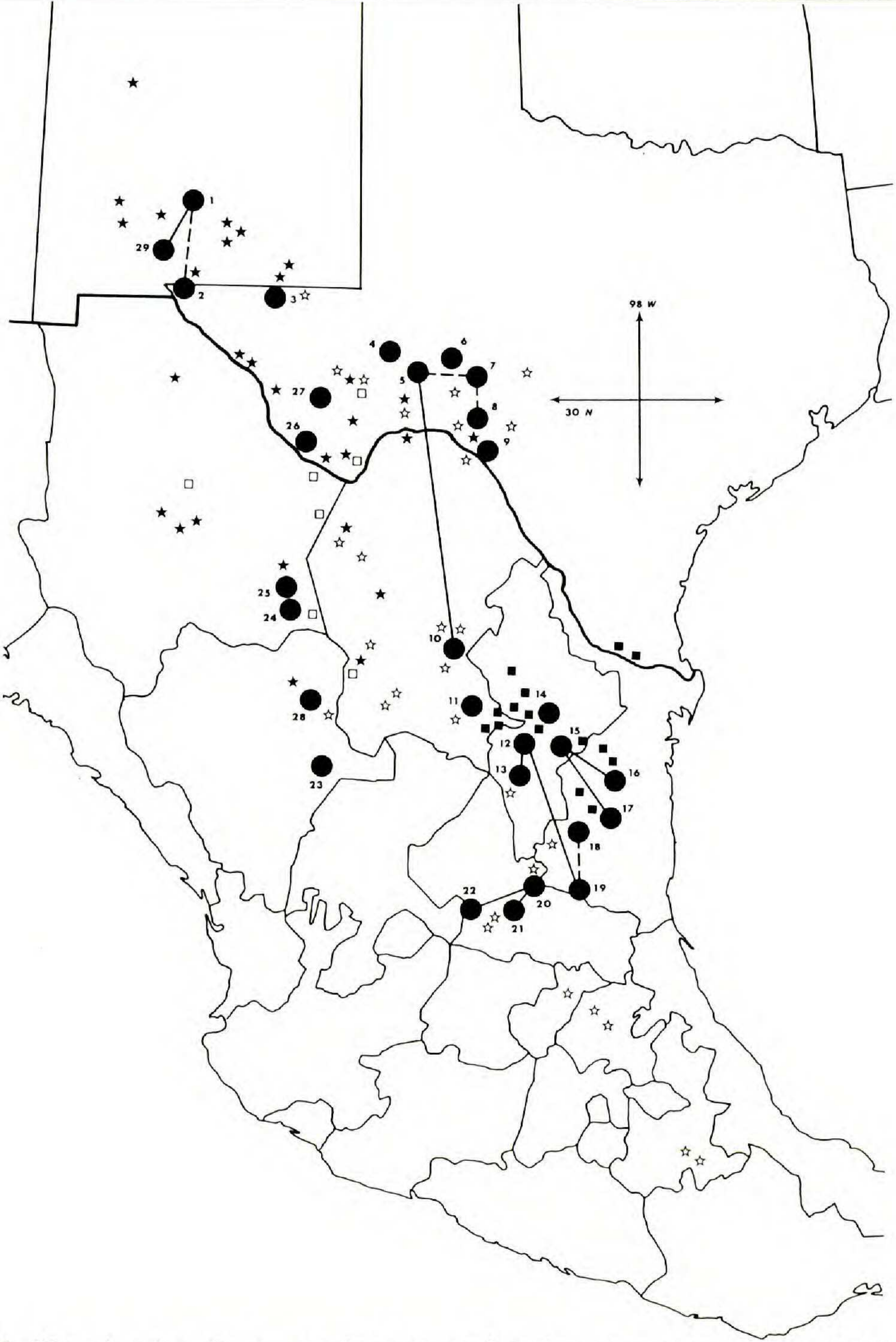

FIG. 4. Map showing the geographic range of *Cyphomeris* and the results of DA. Small symbols represent the locations of selected herbarium specimens and the *a priori* taxonomic group to which they were assigned (see methods). BLACK STARS designate *C. gypsophiloides*. BLACK SQUARES denote *C. crassifolia*. OPEN STARS indicate plants that are more or less intermediate, particularly in leaf width and leaf pubescence. In the north these may be intergrades; in the south they may represent ancestral types. OPEN SQUARES indicate linear-leaved forms of *C. gypsophiloides*. Large BLACK CIRCLES mark the locations of sample populations (Appendix A). Pairs of localities connected by a solid line have values of D^2 that are nonsignificant at $P = 0.05$. Those connected by a dotted line have values that are significant at $P = 0.05$ but not at $P = 0.01$ (see methods).

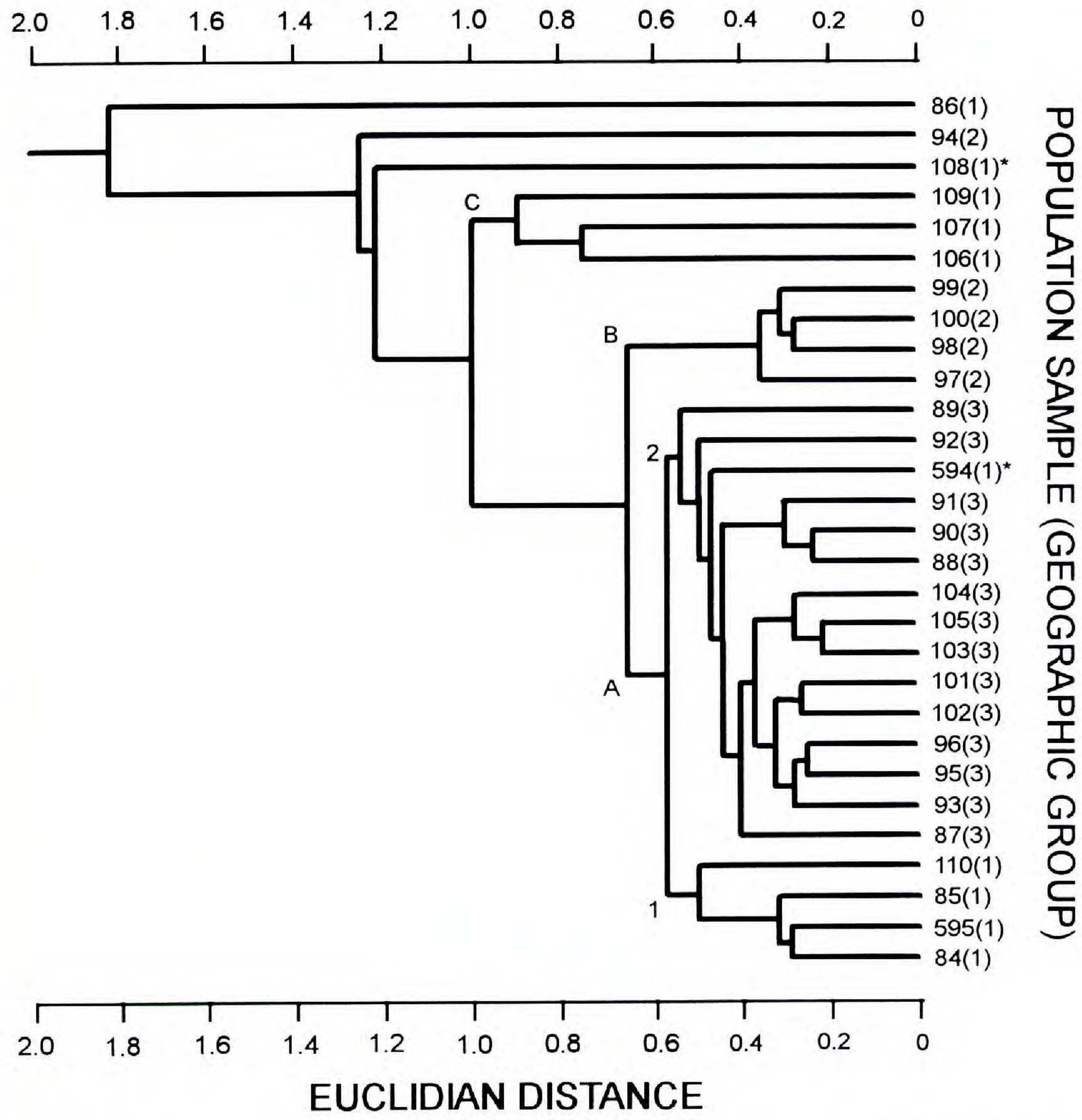

FIG. 5. Dendrogram from the cluster analysis of population samples. Values along the horizontal axis signify the normalized euclidian distance between cluster centroids (SAS Institute 1989). Population localities are identified by the number at the tip of each branch (Appendix A). The values in parentheses indicate the *a priori* group (see caption, Fig. 3) to which each sample was assigned. Clusters discussed in the text are referred to by capital letters and arabic numerals near the base of each cluster. An asterisk at the end of a branch signifies an OTU identified as *C. gypsophiloides* var. *stewartii.*

accounting for 31.5% of the total). The remaining 21 each contribute 7% or less. Eleven characters (ULW, UND, UDP, MLW, HTW, MLR, ULR, PLB, PLW, and HD [Appendix B]), summarizing leaf shape, leaf pubescence, and wartiness of the fruit, load more or less equally on Component 1. Six characters (SLL, PLL, FL, PLW, ULP, and MLP) have high loadings on Component 2. The first four describe overall fruit length; the last two measure petiole length. Aspects of leaf length and width (ULL, MLL, MLPR, ULPR, and MLW) have high loadings on Component 3.

TABLE 1. Character loadings for the first three principal components. The proportion of the total variance accounted for by each component is given in parentheses.

	Loadings		
Character	Component 1 (31.5%)	Component 2 (15.1%)	Component 3 (12.1%)
MLL	-0.2	0.09	0.42
*MLW	0.27	0.14	0.24
MLP	0.21	0.26	0.16
MLPR	-0.19	0.12	0.37
*UND	0.29	-0.04	0.13
*UDP	0.28	0.01	0.16
ULL	-0.17	0.14	0.43
*ULW	0.29	0.12	0.17
ULP	0.22	0.28	0.07
ULPR	-0.14	0.24	0.36
*HD	0.22	-0.16	0.01
GHD	0.1	-0.11	0.08
FLA	-0.14	0.35	-0.15
FDA	0.13	0.15	0.1
FAA	-0.09	-0.17	0.07
*PLL	-0.09	0.35	-0.17
*PLW	-0.23	0.28	-0.12
*PLB	0.23	-0.18	0.06
SLL	0.06	0.37	-0.21
SLW	-0.08	0.21	-0.12
SLB	0.18	0.09	-0.1
*HTW	0.27	-0.04	0.12
*MLR	-0.25	-0.21	0.13
*ULR	-0.26	-0.2	0.16

* Denotes character discussed in the text (see Materials and Methods).

A plot of OTUs of components 1 and 2 reveals three fairly well defined groups (Fig. 6) primarily separated by Component 1; characters UND, UDP, MLW, ULW, HTW, HD, and PLB contribute most. OTUs of *C. crassifolia* form a small cluster to the right of a larger cluster of *C. gypsophiloides* and intergrade OTUS. In comparison to *C. gypsophiloides* OTUs of *C. crassifolia* have leaves that are shorter, wider, more undulate, and more pubescent, and fruits that are shorter and distinctly warty, characters used by Standley (1911) to distinguish the species. OTUs of intergrade and *C. gypsophiloides* var. *stewartii* overlap extensively with OTUs of *C. gypsophiloides* but mostly are distinct from those of *C. crassifolia*. The third cluster (lower left corner of Fig. 6) exhibits a high degree of separation on both components. This group consists of *C. gypsophiloides* OTUs that separate as a result of high values for MLR and ULR combined with low values for MLP and ULP. Little else distinguishes these plants, which occur in widely scattered locations throughout the central Chihuahuan Desert (Fig. 4, open squares). A single outlier, an OTU from the Guadalupe Mountains of western Texas,

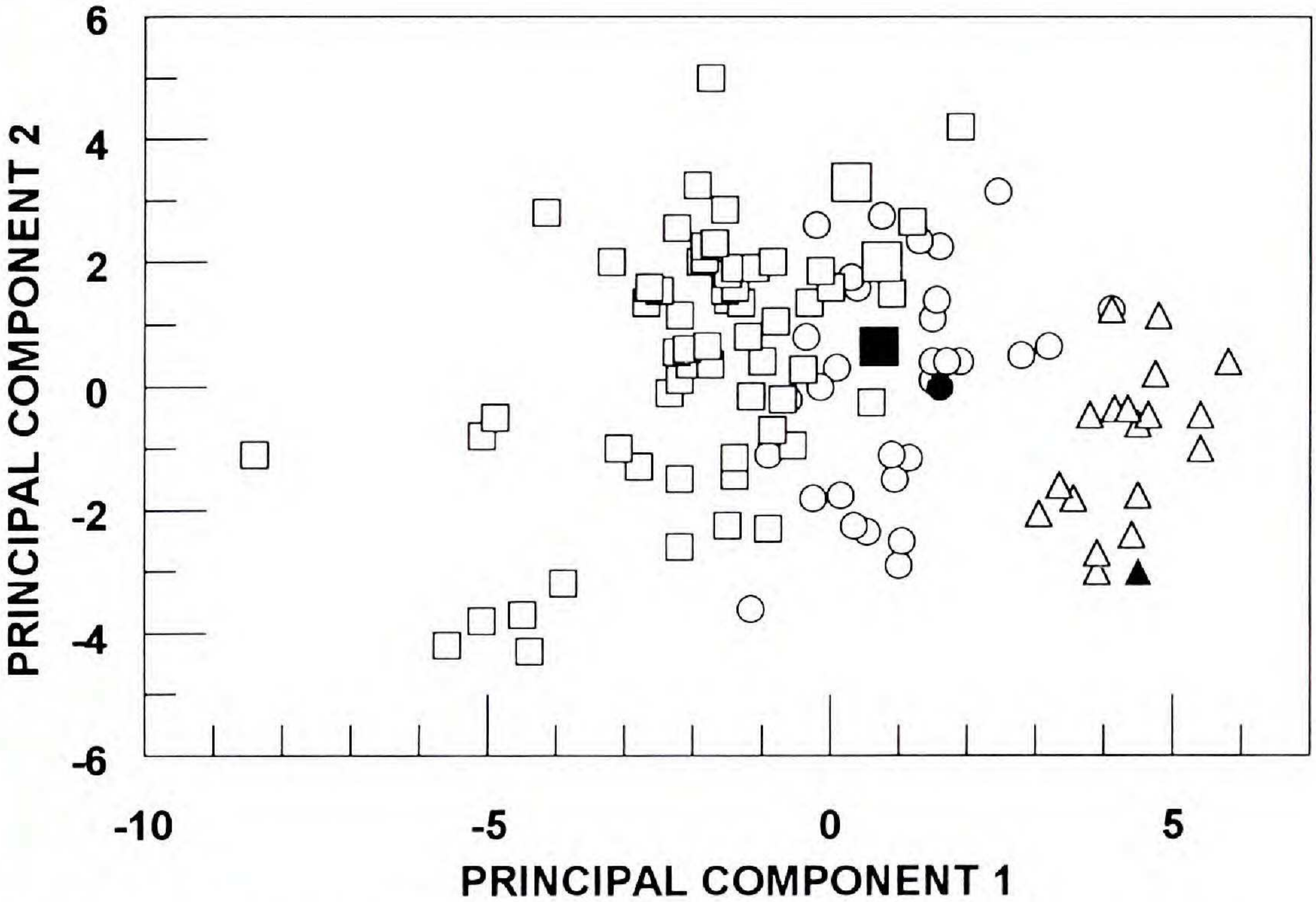

FIG. 6. Plot of specimen OTUs on principal components one and two. Symbols indicate the *a priori* taxonomic group to which each OTU was assigned (squares = *C. gypsophiloides*, triangles = *C. crassifolia*, circles = intergrades). Specimens representing *C. gypsophiloides* var. *stewartii* are indicated by large squares. Type specimens (or, in the case of *C. gypsophiloides*, a specimen collected from near the type locality) are indicated by black figures.

(far left, Fig. 6), has high values of MLR, ULR, FL, PLL, and PLW. It may represent an aberrant individual. It had little affect on the overall results of PCA and CL and was not removed from the analysis.

A similar pattern is produced by a plot of OTUs of components 1 and 3 (Mahrt 1993). *Cyphomeris crassifolia* and *C. gypsophiloides* OTUs form more or less discrete clusters whereas those of intergrades and *C. gypsophiloides* var. *stewartii* overlap extensively with OTUs of *C. gypsophiloides*. A plot of OTUs on components 2 and 3, which primarily measure aspects related to overall size (fruit size for Component 2, leaf size for Component 3), shows little to no separation of *a priori* taxonomic groups (Mahrt 1993) except for two OTUs of *C. gypsophiloides* var. *stewartii*. These show strong separation on Component 3, a reflection of their robust habit and large leaves, attributes noted by Johnston (1944) in the original description of the variety.

Values of D^2 (most are highly significant, $P < 0.01$) for each pair of sample populations are given in Mahrt (1993). Samples joined in Fig. 4 with a solid line have values of D^2 of $P = 0.05$ or greater. Those joined with a dotted line are significant at $P = 0.05$ but not at $P = 0.01$ (Zimmerman and Ludwig 1975). Five groups of interconnected populations are apparent.

TABLE 2. Results of multivariate means separation (see text for explanation of the testing procedure). Samples joined at each step are listed in Appendix A. Significance levels are for the test of populations within groups (Wilks' Lambda).

Group	Samples Combined	Prob. > *F* (Wilks' Lambda)
1	20 with 22	0.64
2	15 with 17	0.61
3	1 with 29	0.7
4	12 with 13	0.36
5	16 with group 2	0.0451*

* Indicates step at which the algorithm was stopped.

The first (samples 1, 2, and 29) consists of three *C. gypsophiloides* populations from New Mexico and Texas. The second (15, 16, and 17) constitutes three populations of *C. crassifolia* from the states of Tamaulipas and Nuevo Leon. The remaining groups are more or less central in distribution and consist entirely of intergrade populations (5, 7, 8, 10, 12, 13, 18, 19, 20, 21, and 22). Populations of *C. gypsophiloides* var. *stewartii* (24 and 28) are distinct from all others in the analysis, including each other. Ten additional population samples are also individually distinct. Five of these (3, 23, 25, 26, and 27) are assigned to *C. gypsophiloides*. Three (4, 6, and 9) are intergrades. The remainder (11 and 14) represent *C. crassifolia*.

Results from the MANOVA indicated significant differences between the centroids of the 29 sample populations (Wilks' Lambda, $P = .001$). The means separation technique resulted in four groups (Table 2). These represent a subset of the results from DA. Groups one and four each consist of two intergrade sample populations. Group two is composed of two *C. crassifolia sample* populations. Group three results from the combination of two *C. gypsophiloides* samples.

DISCUSSION

Results from the CL of population means and the PCA of herbarium specimens indicate that morphological variation in *Cyphomeris* is mostly discontinuous. Two geographically and morphologically defined groups exist, corresponding roughly to the species recognized by Reed (1970) and Standley (1911). The first group comprises *C. crassifolia* from east of the Sierra Madre Oriental, plants characterized by short, warty fruits and short, broad, undulate, moderately to densely pubescent leaves (Fig. 1, a–c). Plants of *C. gypsophiloides* and those designated as intergrades between the two species comprise the second group, an assemblage ranging from southern New Mexico in the United States southward (west of the Sierra Madre Oriental) to the Mexican state of Puebla. They have long, striate fruits and long, narrow, plane to slightly undulate, glabrous to sparsely pubescent leaves. This group can (more or less) be divided into two subgroups. Plants from the northern portion of the range (Fig.1, p–r) usually have glabrous, plane, lanceolate leaves and striate fruits. Intergrade plants (Fig. 1, d–f and j–n) are southern and eastern in distribution, and have sparsely pubescent, lanceolate, plane to slightly undulate leaves and striate to weakly warty fruits. The two forms intermix across western Texas in a more or less clinal fashion.

A third group, consisting of *Cyphomeris gypsophiloides* plants with sessile leaves that have high length to width ratios (Fig. 1, g–i), has no strong geographical unity (Fig. 3, branch C, Fig. 5, branch C). Such plants occur in the widely scattered mountain ranges of western Coahuila, eastern Chihuahua, northeast Durango, and the Big Bend region of Texas.

The CL of herbarium specimens illustrates the problem of the presence of conspicuous variation and the construction of a useful classification in the genus. Twelve individual *Cyphomeris crassifolia* cluster with *C. gypsophiloides* and intergrades (Fig. 3, branch A-2). These plants have large leaves with less pubescence than those of the discrete *C. crassifolia* cluster. Observations of *C. crassifolia* populations in the field suggest certain characters are affected by immediate environmental conditions. Shaded plants tend to have larger, longer, less pubescent leaves with larger length to width ratios than those growing in open sunlight, perhaps resulting in the displacement of *C. crassifolia* specimens by CL. Supporting evidence comes from two sources. First, a CL using only those characters found to be most diagnostic by PCA fully separates the *C. crassifolia* specimens from the *C. gypsophiloides*-intergrade complex, although each group of *C. crassifolia* specimens forms a separate cluster. Second, no displacement occurs in the CL of sample population means, which measures the central tendencies of the respective populations. When these central tendencies are clustered, as opposed to the characteristics of individual specimens, *C. crassifolia* forms a homogeneous group discrete from both *C. gypsophiloides* and intergrades. If the displacement described above is discounted, the CL of herbarium specimens reveals a pattern similar to that from the CL of population samples.

The results from DA and the means separation algorithm show that individual populations of *Cyphomeris* are highly differentiated, most likely due to the effects of selection superimposed on genetic drift resulting from inbreeding and population subdivision, but degree of differentiation varies within the range of the genus (Fig. 4). Populations in the south and east have a higher number of interpopulation connections than those to the north and west. Field observations indicate that populations of *Cyphomeris* in the south and east are less subdivided. In general, they are also characterized by more frequent and dependable rainfall.

Occasionally very different morphs will be found in close proximity. Samples 24 and 25 (Fig. 4) from the Sierra el Diablo, Chihuahua (Appendix A), occur within 1 km of one another and occupy similar habitats (sample 24 comes from slopes with a more southern aspect). Sample 24 has narrow, linear, glabrous leaves (Fig. 1, g–i). In contrast, sample 25 is classic *C. gypsophiloides* var. *stewartii*, with broad, lanceolate, moderately pubescent leaves (Fig. 1, j–l). An extensive search revealed no intergradient plants.

Despite numerous instances of local differentiation, populations of *Cyphomeris* form broadly similar morphological groups with at least some geographic unity, as evidenced by the results of both CL and PCA. Species circumscriptions based on such assemblages are subjective and in general do not represent "real" units in terms of evolution (Ehrlich and Raven 1969). However, they often represent "real" units in terms of geography and ecology, and as such provide the basis for a useful taxonomy. In the case of *Cyphomeris* the most utilitarian approach seems to be division of the genus into two species. *Cyphomeris crassifolia* comprises an entity distinct from the complex formed by *C. gypsophiloides* and the intergrades. The two groups can be separated morphologically by a combination of characters, specifically leaf shape, leaf pubescence, and length and wartiness of the fruit. In addition, the two groups can also be distinguished ecologically. *Cyphomeris crassifolia* is more or less confined to relatively mesic areas east of the Sierra Madre Oriental, and occurs in a variety of settings, from farm fields to subtropical scrub. Densities within a given population are relatively high and the apparent degree of population subdivision relatively low. In contrast, members of the *C. gypsophiloides*-intergrade complex inhabit dry, rocky sites, have low population densities, and a high degree of population subdivision.

Within *C. gypsophiloides* influence of *C. crassifolia* decreases northward and westward across southern Texas in a more or less clinal fashion where suitable habitat for *Cyphomeris* is comparatively undissected but becomes progressively drier. This pattern is particularly evident along southward draining river systems such as the Devil's River. Specimens from the drier limestone rangelands to the north are very much like typical *C. gypsophiloides*, whereas those from the brushy areas at the confluence with the Rio Grande resemble *C. crassifolia*. In general, however, these plants show more affinity to *C. gypsophiloides*. Corresponding with the abrupt habitat changes associated with the Sierra Madre Oriental to the south the two species are relatively sharply delimited.

The existence of subgroups within *C. gypsophiloides* (Fig. 3 and Fig. 5, branches A-1 and A-2) suggests that infraspecific taxa might be recognized. It is not clear, however, whether intergradient plants result from of primary intergradation or secondary contact between northern representatives of *C. gypsophiloides* and *C. crassifolia*, or both. Widely accepted hypotheses of the northward expansion of the Chihuahuan Desert and the evolution of the Mexican flora suggest that the southern intermediate types (from San Luis Potosi south to Puebla) represent an ancestral form that gave rise to the northern, more or less glabrous, component of *C. gypsophiloides* and the eastern, very pubescent *C. crassifolia*. The latter two groups may have then met secondarily to produce the northern intergrades found from Coahuila north to western Texas. Some evidence exists for this. A single population (sample 96) that appears to represent a hybrid swarm has been documented from central Nuevo Leon. Plants in this population exhibit almost the entire range of leaf variation, from plane, glabrous, lanceolate leaves to examples that are undulate, pubescent, and rhombic. The collection *Spellenberg, Zimmerman, and Zucker* 8374, MEXICO. Coahuila: Cuesta de la Muralla, N of Saltillo, 11 Oct 1985, (NMC) is even more suggestive, combining the leaf characters of *C. gypsophiloides* (plane, glabrous, lanceolate leaves) with the short, warty fruits of *C. crassifolia*. Until a more thorough understanding is gained of both the nature and extent of apparent hybridization, and also of local differentiation that results in such extreme leaf types as the linear glabrous leaves in many scattered populations or the large pubescent leaves of robust plants in the local phased named as the var. *stewartii*, we do not recommend formal recognition of infraspecific taxa.

TAXONOMY

Cyphomeris Standl., Contr. U.S. Nat. Herb. 13:428. 1911. *Lindenia* Mart. & Gal., Bull. Acad. Sci. Brux. 10:358. 1843. *Tinantia* Mart. & Gal., Bull. Acad. Sci. Brux. XI:240. 1844. *Senkenbergia* Schauer, Linnea 19:711. 1847.

Perennial herbs with woody taproots, glabrous to densely pubescent with pale, curved, bristle-like to capitate glandular hairs. *Stems* divaricately branched, erect, ascending, trailing or clambering through shrubs, to 2m, often brittle, upper internodes much longer than the lower ones, each internode with a glutinous band near the midpoint. *Leaves* opposite, those at a node unequal, exstipulate, petiolate or rarely sessile, weakly succulent; blades linear to lanceolate, ovate, broadly oblong, or rhombic, entire or undulate. *Inflorescences* axillary or terminal racemes; pedicels subtended by a lanceolate, sparsely ciliate, caducous bract 2.5–6 mm long; pedicels 0.5–1 mm. *Flowers* chasmogamous or cleistogamous. *Perianth* of chasmogamous flowers pale pink to red-violet (rarely greenish-white), broadly funnelform from a short, weakly curved tube constricted above the ovary; limb slightly oblique, 5 lobed, lobes emarginate. *Stamens* 5, exserted. *Pistil* unicarpellate; style filiform, exserted beyond the anthers; stigma capitate. Anthocarp stipitate, clavate, gibbous on the dorsal side, generally concave ventrally, pendant or refracted, longitudinally striate with 10 fine striations and/or series of elongate interrupted ridges, exuding mucilage when wetted from conspicuous wart-like protuberances.

In its racemose inflorescence and clavate fruits *Cyphomeris* resembles some species of *Boerhavia* and has been retained in that genus by F. R. Fosberg (1978).

TYPE SPECIES: *Cyphomeris gypsophiloides* (Mart. & Gal.) Standl.

KEY TO THE SPECIES OF *CYPHOMERIS*

1. Leaves glabrous or sparsely pubescent, blades lanceolate to linear, less than one half as wide as long, entire to shallowly undulate; anthocarps 8–11 mm, striate to weakly warty .... *C. gypsophiloides*
1. Leaves pubescent, blades ovate, broadly oblong, or rhombic, greater than one half as wide as long, undulate; anthocarps 6–8 mm, prominently warty, especially on dorsal side .... *C. crassifolia*

1. Cyphomeris gypsophiloides (Mart. & Gal.) Standl., Contr. U.S. Natl. Herb. 13:428. 1911. TYPE: MEXICO. OAXACA: Plains near Tehuacan, *Galeotti 577* (HOLOTYPE: BR!). *Lindenia gypsophiloides* Mart. & Gal., Bull. Acad. Sci. Brux. 10:358. 1843. *Tinantina gypsophiloides* (Mart. & Gal.) Mart. & Gal., Bull. Acad. Sci. Brux. 11:240. 1844. *Senkenbergia gypsophiloides* (Mart. & Gal.) Benth. & Hook., Gen. Pl. 3:6. 1880. *Boerhavia gypsophiloides* (Mart. & Gal.) Coulter, Contr. U.S. Natl. Herb. 2:354. 1894.

Senkenbergia annulata Schauer, Linnea 19:711. 1847. TYPE: Mexico: location unknown, *Aschenborn exs.* #253 (not seen).

Boerhavia gibbosa Pavon ex Choisy in DC. Prodr. 13:457. 1849, nom. non leg.

Plants glabrous to sparsely pubescent with pale curved, occasionally gland-tipped hairs primarily along the stems and the veins of leaves. *Stems* erect to ascending, 0.5–1.5 m. *Leaves* broadly oblong-lanceolate to narrowly lanceolate or rarely, linear (and then sub-sessile), less than one half as wide as long, the distal blades much broader than the proximal (except in linear leaved forms), proximal blades 1–9 cm × 1–30 mm, entire to shallowly undulate. *Perianth* light pink to red violet, 7–10 mm above the ovary. *Anthocarp* 8–11(–14) mm, striate to weakly warty, usually gibbous.

Distribution.—Southern New Mexico and western Texas in United States south to the Mexican states of Puebla and Oaxaca; rocky soils of washes, slopes, and roadsides, common on limestone, desertic scrub to open and dry pine-oak woodland; 500–2500 m. Blooming from mid-April to early November, but mostly mid-summer to early fall. Highly variable (Fig. 1, d-f, g-i, m-o, p-r).

The holotype of *C. gypsophiloides* is fragmentary, consisting only of a leafless branch and several semi-mature fruits, making most of its original character states impossible to determine. The collection *Chiang et. al. 2265* (MEXICO. Puebla: Plateau of San Lorenzo, near Tehuacan, 7 Aug 1981, [TEX]) comes from very near the type locality. It has the elliptic-lanceolate, slightly pubescent leaves, and moderately warty fruits that are characteristic of southern intermediate plants (Fig. 1, m-n).

2. **Cyphomeris crassifolia** (Standl.) Standl., Contr. U.S. Natl. Herb.13:428. 1911. TYPE: MEXICO. COAHUILA: Saltillo and vicinity, *Palmer 172* (HOLOTYPE: UC!; ISOTYPES: F, G!, MO!, NY!, US!). *Senkenbergia crassifolia* Standl., Contr. U.S. Natl. Herb. 12:373. 1909.

Plants finely pubescent with pale, curved hairs (rarely capitate glandular). *Stems* ascending to trailing, 0.5–2.0 m. *Leaves* rhombic to ovate or broadly oblong, one half as wide as long or wider, the distal blades nearly as broad as the proximal ones, proximal blades 1–5 cm × 8–40 mm, undulate and coarsely sinuate lobed or rarely more or less entire. *Perianth* pale pink (rarely greenish-white) to deep pink or red-violet, 6–8 mm above the ovary. *Anthocarp* 6–8(–11) mm, usually strongly gibbous, prominently warty, especially on dorsal side.

Distribution.—Extreme southern Texas in the United States and parts of Nuevo Leon and Tamaulipas in Mexico, primarily east of the Sierra Madre Oriental; fine or rocky soils on flats, washes, slopes, and roadsides, desertic scrub, more common in fallow fields and in semiarid or subtropical scrub; 1200 to 2500 m. Blooming mid-April to mid-December, but mostly late summer to late fall. Compared to *C. gypsophiloides*, *C. crassifolia* comprises a more cohesive, well defined morphological unit (Fig. 1, a-c) occurring in relatively mesic habitats and often having high population densities. It is likely that this species hybridizes with *C. gypsophiloides* (see discussion, preceding). As a result, populations exhibiting various degrees of intermediacy can be expected, particularly along the northern edge of the Sierra Madre Oriental where the geographic barriers to gene flow are less pronounced.

In southern Texas, at the northern limit of the species' range, *C. crassifolia* is known from only two collections; Starr Co., NW of Roma, 17 Dec 1963, *Wood 723* (TEX) and between Sullivan City and Rio Grande, 13 Apr 1941, *Runyon 2547* (TEX US).

APPENDIX A

List of population samples. Bold numbers at the beginning of each citation indicate the sample number (Fig. 5). Italicized numbers following each citation and adjacent to parentheses refer to the *a priori* group to which the sample was assigned (1 = *C. gypsophiloides*, 2 = *C. crassifolia*, 3 = intergrade). Samples representing *C. gypsophiloides* var. *stewartii* are marked with an asterisk. Numbers in parentheses indicate the sample size. Unless otherwise noted all collections are those of Mahrt and various associates. Vouchers are deposited at NMC. Duplicates are widely distributed.

29—UNITED STATES, New Mexico. Doña Ana Co.: W slope of Organ Mtns, 17.6 air km E of Las Cruces, *Spellenberg 5953*, *1*(10). 1—Socorro Co.: White Sands Missile Range, San Andres Mtns., 60 km NE of Truth or Consequences, 29 Jul 1990, *84 1*(9). 6 Texas. Crockett Co.: 6.4 km SE of Sheffield, 12 Oct 1990, *89 3*(10). 2—El Paso Co.: Franklin Mtns., 0.4 km E of Trans Mountain Road pass, 11 Oct 1990, *85 1*(10). 3—Hudspeth Co.: Guadalupe Mtns., 8 km SW of Pine Springs, 12 Oct 1990, *86 1*(10). 27—Jeff Davis Co.: 16 km SE of Fort Davis, 21 Oct 1990, *110 1*(10). 4—Pecos Co.: 22.4 km E of Bakersfield, 12 Oct 1990, *87 3* (10); 5—89.6 km E of Fort Stockton, 12 Oct 1990, *88 3*(9). 26—Presidio Co: 4.8 km S of Shafter, 21 Oct 1990, *109 1*(6). 7—Val Verde Co.: 88 km NW of Del Rio, 13 Oct 1990, *90 3*(9); 8—28.8 km N of Comstock, 13 Oct 1990, *91 3*(10); 9—19.2 km NW of Del Rio, 13 Oct 1990, *92 1*(10).

24—MEXICO. Chihuahua: Sierra el Diablo, 80 km E of Jimenez, 19 Oct 1990, *107 1*(10); 25—Sierra el Diablo, 80 km E of Jimenez, 20 Oct 1990, *108 1**(10). 10—Coahuila: Sierra la Gavia, 33 km S of Monclova, 14 Oct 1990, *93 3*(10); 11—27.2 N of Saltillo, 14 Oct 1990, *94 2*(10). 23—Durango: 17.6 km S of Cuencame, 18 Oct 1990, *106 1*(10); 28—N end of Sierra el Rosario, 20 km SW of Mapimi, *Spellenberg 5947*, *1**(10). 12—Nuevo Leon: Sierra Madre Oriental, 16.6 km W of Iturbide, 15 Oct 1990, *95 3*(10); 13—Sierra Madre Oriental, 14.4 km W of Iturbide, 15 Oct 1990, *96 3*(10); 14—11.2 km S of Montemorelos, 15 Oct 1990, *97 2*(10); 15—14.4 km S of Linares, 15 Oct 1990, *98 2*(10). 20—San Luis Potosi: 110 km NE of San Luis Potosi, 16 Oct 1990, *103 3*(9); 21—38 km NE of San Luis Potosi, 16 Oct 1990, *104 3*(10); 22—33.6 km W of San Luis Potosi, 17 Oct 1990, *105 3*(10). 16—Tamaulipas: 9.6 km N of El Barretal, 15 Oct 1990, *99 2*(10); 17—E slope of Sierra Madre Oriental, 9.6 km SW of Ciudad Victoria, 16 Oct 1990, *100 2*(10); 18—W slope of Sierra Grande, Sierra Madre Oriental, 27.2 km NE of Jaumave, 16 Oct 1990, *101 3*(10); 19—Sierra Madre Oriental, 16 km SW of Jaumave, 16 Oct 1990, *102 3*(9).

APPENDIX B

Characters measured for multivariate analysis of *Cyphomeris*. The letter in parentheses refers to scoring method (m = mensural, c = meristic). Units of measurement are indicated for mensural characters. Unless otherwise noted, fruit measurements are in ocular units at 10×. Primary line measurements were taken on the first lateral line of fruit. Secondary line measurements were recorded for the secondary line directly beneath the primary line.

VEGETATIVE CHARACTERS: GHD (c)—total number of gland tipped hairs in a 1.5 × 2 mm square at 25×; HD (c)—total number of hairs in a 1.5 × 2 mm square at 25×; MLL (m)—mid leaf length, in mm; MLP (m)—length of mid leaf petiole, in mm; MLPR (m)—distance from tip of mid-leaf to widest point, in mm; MLR (m)—ratio of MLL to MLW; MLW (m)—mid-leaf width, in mm; ULL (m)—upper leaf length, in mm; ULP (m)—length of upper leaf petiole, in mm; ULPR (m)—distance from the tip of upper leaf to widest point, in mm; ULR (m)—ratio of Ull to ULW; ULW (m)—upper leaf width, in mm; UDP (c)—depth of deepest undulation; UND (c)—number of undulations along right margin of mid leaf. FRUIT CHARACTERS: FA (m)—fruit angle, in degrees; FD (m)—depth of fruit, distance from the dorsal to ventral surface; FL (m)—length of fruit; HTW (m)—height of tallest wart on ventral surface, in ocular units at 25×; PLB (c)—number of breaks in primary line; PLL (m)—length of primary line; PLW (m)—length of longest wart of primary line; SLB (c)—number of breaks in secondary line; SLL (m)—length of secondary line; SLW (m)—length of longest wart of secondary line.

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